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SHORT COMMUNICATION

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Conflict and postconflict behaviour in captive black-and-white snub-nosed monkeys (*Rhinopithecus bieti*)

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Abstract Black-and-white snub-nosed monkeys (*Rhinopithecus bieti*) have almost never been the subject of any behavioural observations in captivity. This study was aimed at providing preliminary information about agonistic and reconciliation behaviour in a group kept at the Kunming Institute of Zoology in China. Established procedures were used for this investigation (i.e., the postconflict/matched-control method and the time-rule method). Intra-group aggression rates were quite low. Postconflict affiliation as well as selective attraction of former opponents to each other following conflicts was demonstrated. Former opponents contacted each other earlier in postconflict periods than in matched-control periods. The average conciliatory tendency of all focal individuals combined was 54.5%. After an agonistic interaction, the first affiliative contact between former aggressors usually took place within the first minute. The behaviours most often shown as first affiliations after a conflict were body contact, mount, touch, and "hold-lumbar", of which the latter is an explicit reconciliatory gesture. Furthermore, the adult male intervened non-aggressively in 84% of all conflicts ($n = 25$) among the adult females. Overall, the patterns of aggression and reconciliation observed in *R. bieti* bear many of the traits that characterise tolerant primate species.

Keywords *Rhinopithecus* · Captivity · Aggression · Reconciliation · Male policing

Introduction

The black-and-white snub-nosed monkey (*Rhinopithecus bieti* Colobinae) is a highly endangered primate species that inhabits mountainous forests in northwest Yunnan and southeast Tibet (Long et al. 1994). Only recently has it been found that they live in large, cohesive, multilevel groups that are composed of one-male units (Kirkpatrick et al. 1998). There exist almost no behavioural studies of this species in captivity.

The study of aggression and conflict management provides useful information to qualify social relationships within primate groups. Reconciliation or postconflict (PC) affiliation is defined as the affiliative contact occurring after conflict between former opponents (de Waal and van Roosmalen 1979). Reconciliation is assumed to be a mechanism to repair a relationship that has been disrupted by a conflict (Aureli and van Schaik 1991; Cords 1992). Reconciliation has been documented in a wide variety of primate taxa, but, compared with the cercopithecines, PC studies in colobines are underrepresented (for a review see Aureli et al. 2002). Studies of reconciliation in primates have shown a relationship between the "dominance style" of a given species and the proportion of conflicts that are reconciled, that is, egalitarian or tolerant species have higher frequencies of reconciliation than despotic species (de Waal 1989). In general, colobines are more egalitarian and have less pronounced dominance hierarchies than cercopithecines (Struhsacker and Leland 1987) and are thus expected to reconcile at higher rates. The egalitarianism of colobines is best explained by weak within-group feeding competition due to their mostly folivorous diet (Yeager and Kirkpatrick 1998). The goal of this study was to determine the overall patterning of agonistic behaviours in captive *R. bieti* and to investigate whether PC affiliation exists.

Methods

Subjects and housing

The study was carried out between August and October 2002 on one group of *R. bieti* at the breeding centre of

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the Kunming Institute of Zoology (KIZ), China. During the day, the animals were kept in two outdoor cages (66 m^2×4 m) separated by a grid. Subgroup A consisted of one adult male, two adult females, one juvenile male, and one juvenile female, and subgroup B of one subadult male, two juvenile males, and one juvenile female.

Data collection and analysis

The total observation time of the study group was 210 h. Agonistic interactions within subgroups involving individuals over 1 year of age were recorded using "all occurrence sampling" (Altmann 1974). An agonistic interaction was defined as the display of an aggressive behaviour by an individual (threat, chase, contact aggression) followed by a response of the victim such as avoidance, screech, or counter-aggression. For each agonistic interaction, I noted the identities of the aggressor and victim.

The PC observational procedure is based on de Waal and Yoshihara (1983). The PC observation lasted for 10 min and was started after the last aggressive behaviour had been exchanged. If the conflict flared up again within 2 min of the PC, the PC observation was restarted. One of the opponents was followed as the focal; the numbers of aggressors and recipients as focals were balanced. In case of polyadic conflicts, only the initial conflict dyad was counted. During the PC, all affiliative interactions were noted together with the identities of the involved individuals and of the initiator. Affiliative contacts were defined as embrace, touch, groom, present, play, mount, assert, body contact, and "hold-lumbar". A 10-min matched-control observation (MC) was made on the next possible day, at the same time, following the same focal individual. If the focal individual was involved in an agonistic interaction within 2 min before a planned MC, or in the first 2 min of an ongoing MC, the MC was postponed until the next possible day.

To compare PC and MC periods, the 30-s block in which the first non-aggressive contact occurred between former opponents is taken into account. The PC/MC pair is called "attracted" if the affiliative interaction occurs earlier in the PC than in the MC periods, "dispersed" when it occurs earlier in the MC than in the PC periods, and "neutral" when it occurs during the same 30-s block or when no contact occurs in either the PC or the MC periods. A skew in favour of attracted pairs indicates that reconciliation is performed. This analysis is referred to as the "PC–MC method" (de Waal and Yoshihara 1983). Conciliatory tendencies (CT) were calculated for each focal individual using the index designed by Veenema et al. (1994): CT = 100×(attracted pairs−dispersed pairs)/(all pairs). To determine the timing of reconciliation, the "time-rule method" (Aureli et al. 1989) was used: I determined in which minute block the first interopponent contact occurred in every PC and MC sample. Then I compared the distribution over time of the PC contacts with the distribution in the MCs.

Results

A total of 116 PC–MC pairs were analysed. The overall mean frequency of agonistic interactions per individual and hour was 0.30. Thirty-five percent of the conflicts were polyadic, 65% dyadic. Seventy-two percent of the observed conflicts involved unidirectional aggression, 28% bidirectional aggression.

After a conflict, reconciliation was demonstrated following the PC–MC method since a higher proportion of opponents were attracted than were dispersed (70.1% attracted, 9.5% dispersed; Wilcoxon matched-pairs test, $n = 8$, $T = 0$, $P < 0.005$, one-tailed). The average CT of all focal individuals combined was 54.5% (±18.7% SD). According to the time rule, former opponents contacted each other earlier in PCs than in MCs. There was a significant difference in the distribution over time of the first affiliative interaction between former opponents in the PCs and in the MCs (Kolmogorov–Smirnov test, $D = 0.605$, $P < 0.001$), and the greatest distance in the cumulative distributions was within the first minute (Fig. 1). This was confirmed at the individual level for the first minute of PC and MC, respectively (Wilcoxon matched-pairs test, $n = 8$, $T = 0$, $P < 0.01$). To rule out that the attraction between former opponents was merely the result of a general increase in affiliation between group members (de Waal and Yoshihara 1983), it was tested whether the opponents showed selective attraction towards each other. Focal subjects are expected to preferentially affiliate with former opponents during PC, but not MC. This was the case, as the mean selective attraction for the PCs was 44.0% (±6% SD) as compared to 29.0% (±17% SD) for the MCs (Wilcoxon matched-pairs test, $n = 8$, $T = 3$, $P < 0.05$).

The behaviours most often shown as first affiliation after a conflict were body contact ($n = 35$), mount (14), touch (10), and "hold-lumbar" (8; Fig. 2). The victim was the initiator of first affiliative PC contacts in 49% of the cases and the aggressor in the remaining 51%.

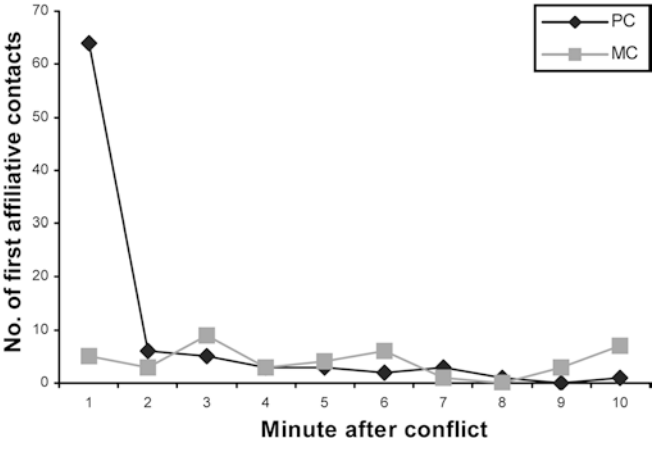

Fig. 1 The number of first affiliative contacts between former opponents in the 10-min period following an agonistic interaction. *PC* postconflict, *MC* matched-control period

Fig. 2 "Hold-lumbar" gesture in *Rhinopithecus bieti*, performed by the subadult male on the *left* and received by the juvenile female on the *right* (photo Cyril C. Grüter)

The adult male intervened peacefully in 84% of all conflicts ($n = 25$) among the adult females. In 16 cases, a behaviour of the sexual repertoire took place right after the intervention, that is, either a copulation between the male and one or both of his females, or female proceptive crouching. In 4 cases, the male interposed itself between the females.

Discussion

The occurrence of postconflict affiliation as well as selective attraction of former opponents following a conflict was demonstrated in captive *R. bieti*. This is in accordance with findings of the other colobine studies in captivity (Ren et al. 1991; Björnsdotter et al. 2000; Arnold and Barton 2001). The high proportion of reconciled conflicts reported for *R. roxellana* (Ren et al. 1991) and for *R. bieti* (present study) places snub-nosed monkeys amongst the most conciliatory primate taxa. After an agonistic interaction, the first affiliative contact between former opponents usually took place within the first minute, which is in general agreement with previous reports for other reconciling species (Kappeler and van Schaik 1992). Conciliatory tendencies, however, may be subject to intraspecific variation (Castles et al. 1996). Hence caution is warranted when attributing these findings to other groups.

Most primate species use no particular behaviour pattern to reconcile (e.g., York and Rowell 1988), but others use special "explicit" gestures rarely shown outside the PC context (de Waal and Ren 1988). Mounting was significantly more often used by *R. bieti* in the context of reconciliation. "Hold-lumbar" also appears to be an "explicit" reconciliatory behaviour that has been described for *R. roxellana* (Ren et al. 1991) and in a slightly modified version for *Macaca arctoides* (de Waal and Ren 1988). Open-mouth display was the most common affiliative behaviour after conflicts in *R. roxellana* (Ren et al. 2000), whereas it was virtually absent in *R. bieti*.

Peace-making strategies have been found in primate species living in different social organisations such as multimale–multifemale groups and one-male groups (see Aureli et al. 2002). The social organisations of both *R. bieti* and *R. roxellana* are based on harems (Kirkpatrick et al. 1998; Ren et al. 2000), and the overall striking similarities in postconflict behaviour between these two closely related species is an indication for possible similarities in underlying social mechanisms that hold the group together. The fact that agonistic patterns and postconflict behaviours are related to the constraints of the social organisation of a species has been demonstrated by covariation studies of social characteristics among social organisations of macaques (Thierry 2000).

High rates of reconciliation in catarrhine primates may be at least partly artefacts of captivity (Sommer et al. 2002). Only one systematic PC study on colobines has been undertaken in the field, where hanuman langurs (*Semnopithecus entellus*) usually avoided each other after conflicts (Sommer et al. 2002). Given the large amount of space available in the wild as opposed to a captive setting, temporary escape from other group members as a form of dispersive conflict resolution—in contrast to active reconciliation—may also be an option in free-ranging *R. bieti*. So far, no information about PC affiliation in wild *R. bieti* is available. However, wild *R. roxellana* perform affiliative PC behaviour patterns such as embrace and "hold-lumbar" in the wild (Ren et al. 2000; personal observation).

The adult male made non-aggressive interventions in most conflicts between the adult females, often engaging in mounts or copulations. Such male policing behaviour including mounting has also been reported for *R. roxellana* (Ren et al. 1991) and *Papio hamadryas* (Zaragoza and Colmenares, unpublished, cited in Colmenares et al. 2000). It seems likely that *R. bieti* males engage in sexual behaviour with females as a means of regulating tensions. Peaceful male interventions might reinforce female loyalty and can ultimately be considered as a form of male mating effort (Watts et al. 2000).

Overall, the patterns of aggression and reconciliation observed in *R. bieti* bear many of the features that characterise tolerant species: intragroup aggression rates were quite low, severe aggression was absent, bidirectional conflicts were common, initiative of victims to reconcile was frequent, CTs were high compared to cercopithecines, and specific gestures were often used to initiate PC affiliation.

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